Natural selection and variation

By Muhammad Irfan Jalali

https://www.youtube.com/irfanrajput

This tutorial first establishes the conditions for natural selection to operate, and distinguishes directional, stabilizing, and disruptive forms of selection. We then consider how widely in nature the conditions are met, and review the evidence for variation within species; the review begins at the level of gross morphology and works down to molecular variation. Variation originates by recombination and mutation, and we finish by looking at the argument to show that when new variation arises it is not 'directed' toward improved adaptation.

The struggle for existence

Organisms produce more offspring than - given the limited amounts of resources - can ever survive, and organisms therefore compete for survival. Only the successful competitors will reproduce themselves. It was Charles Darwin (opposite) who first discussed this competition and described it as the "struggle for existence". The struggle for existence takes place within a web of ecological relations. Above an organism in the ecological food chain, there will be predators and parasites, seeking to feed off it; and below it are the food resources it must in turn consume in order to stay alive. At the same level in the chain are competitors, which may be competing for the same limited resources of food, or space. An organism competes most closely with other members of its own species, because they have the most similar ecological needs to its own; other species, in decreasing order of ecological similarity, also compete and exert a negative influence on the organism's chance of survival.

Why aren't the oceans overrun by Atlantic cod?

The Atlantic cod (*Gadus callarias*) is one of the most fecund of vertebrates. Female cod lay their eggs on the surface of the water; as soon as they are discharged, a slaughter begins, as can be seen in the graph opposite. A negligible proportion of the 5 million or so eggs laid by a female cod in her lifetime will survive and reproduce: an average female in the cod population will produce only two successful offspring.

This figure, that on average two eggs per female survive to reproduce successfully, is not the result of an observation: it comes from a logical calculation. Only two can survive, because any other number would be unsustainable over the long term. It takes a pair of individuals to reproduce. If an average pair in a population produce less than two offspring, the population will soon go extinct; if they produce more than two on average, the population will rapidly reach infinity - which is also unsustainable. So, if two is the optimum number of offspring to maintain the population, why do females produce the other 4,999,998 eggs?

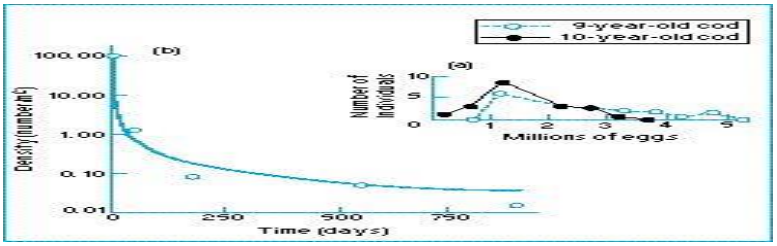

Figure: mortality of cod in their first two years of life. From Cushing (1975)

Why does this excess fecundity exist?

The condition of 'excess' fecundity - females produce more offspring than survive - is universal in nature. In every species, more eggs are produced than can survive to the adult stage. The cod dramatizes the point in one way, because its fecundity, and mortality, are so high; but the same point is true for species which have lower reproductive rates. Darwin once famously calculated that even the slow breeding elephant (pictured opposite) produces far more offspring than could ever hope to reach maturity.

This excess fecundity exists because there are inadequate resources in nature to support all the eggs that are laid and all the young that are born. There are only limited amounts of food and space in the world; a population can expand but there will come a point beyond which the food supply must limit its further expansion. Thus, members of a population, and members of different species, compete in order to survive, and this follows from the conditions of limited resources and excess fecundity.

The conditions for natural selection

The excess fecundity, and consequent competition to survive in every species, provide the preconditions for the process Charles Darwin called natural selection. Natural selection is easiest to understand, in the abstract, as a logical argument, leading from premises to conclusion. The argument, in its most general form, requires four conditions:

1. Reproduction. Entities must reproduce to form a new generation.

2. Heredity. The offspring must tend to resemble their parents: roughly speaking, 'like must produce like'.

3. Variation in individual characters among the members of the population. If we are studying natural selection on body size, then different individuals in the population must have different body sizes.

4. Variation in the fitness of organisms according to the state they have for a heritable character. In evolutionary theory, fitness means the average number of offspring left by an individual relative to the number of offspring left by an average member of the population. This condition therefore means that individuals in the population with some characters must be more likely to reproduce (i.e., have higher fitness) than others.

If these conditions are met for any property of a species, natural selection automatically results. And if any are not, it does not.

Thus entities, like planets, that do not reproduce, cannot evolve by natural selection; entities that reproduce but in which parental characters are not inherited by their offspring also cannot evolve by natural selection. But when the four conditions apply, the entities with the property conferring higher fitness will leave more offspring, and the frequency of that type of entity will increase in the population.

Richard Dawkins gives his own definition of the conditions for natural selection. "Natural selection will operate wherever there is heredity, variation, and that will almost inevitably follow given you have got heredity, competition - and that will almost inevitably follow given you have got heredity and variation. So, I suspect that the conditions for natural selection to work are very minimal indeed: namely, the existence of the phenomenon of heredity."

Types of natural selection

We can distinguish three kinds of natural selection, according to their effect on a character such as body size.

• Directional selection

Smaller individuals may have higher fitness (i.e. produce more offspring) than larger individuals. Natural selection is then directional: it favours smaller individuals and will, if the character is inherited, produce a decrease in average body size. Directional selection could, of course, also produce an evolutionary increase in body size if larger individuals had higher fitness.

An example of directional selection: pink salmon

Pink salmon (*Onchorhynchus gorbuscha*) in the Pacific Northwest have been decreasing in size in recent years. In 1945, fishermen started being paid by the pound, rather than per individual, for the salmon they caught and they increased the use of gill netting, which selectively takes larger fish. After gill netting was introduced, smaller salmon had a higher chance of survival; the selection favouring small size in the salmon population was intense, because fishing is thorough: about 75 - 80% of the adult salmon swimming up the rivers under investigation were caught in these years. The average weight of salmon duly decreased, by about one-third, in the next 25 years.

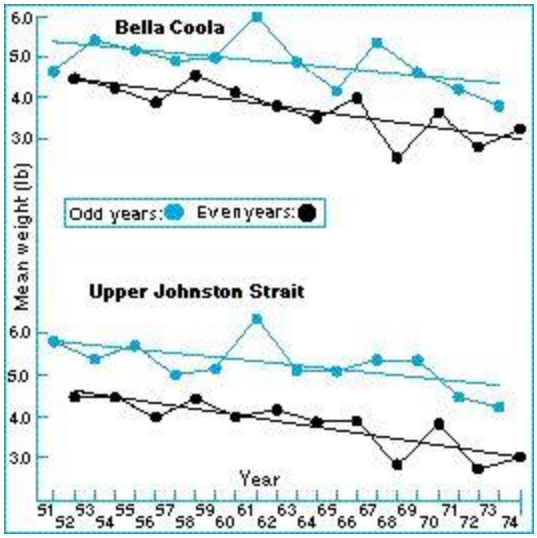

Figure: the graph shows the decrease in size of pink salmon in two rivers in British Columbia. Two lines are drawn for each river: one for the salmon caught in odd-numbered years, the other for even years. Salmon caught in odd years are presumably heavier because of the two-year life cycle of the salmon. From Ricker (1981).

• Stabilizing selection

Natural selection could be stabilizing. The average members of the population, with intermediate body sizes, may have higher fitness than the extremes.

An example of stabilizing selection: birth weight in humans

Studies of birth weight in humans have provided good examples of stabilizing selection: the graph illustrates a classic result for a sample in London, UK, in 1935 - 1946 and similar results have been found in New York, Italy, and Japan. Babies that are heavier or lighter than average did not survive as well as babies of average weight.

Stabilizing selection has probably operated on birth weight in human populations from the time of the evolutionary expansion of our brains about 1 - 2 million years ago until the 20th century. In most of the world it still does. However, in the 50 years since Karn and Penrose's study, the force of stabilizing selection on birth weight has relaxed because of improved care for premature deliveries (the main cause of lighter babies) and increased frequencies of Caesarean deliveries for babies that are large relative to the mother (the lower survival of heavier babies was mainly due to injury to the baby or the mother during birth). Now, in the 1990s in wealthy countries, the stabilizing selection that had been operating on human birth weight for over a million years has all but disappeared.

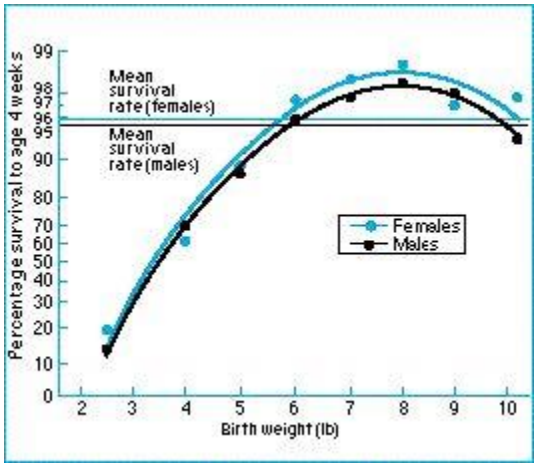

Figure: stabilizing selection on human birth weight. Infants weighing 8 lb at birth have a higher survival rate than heavier or lighter infants. The graph is based on infants born in London from 1935 to 1946. From **Karn** and **Penrose** (1951).

• Disruptive selection

Natural selection could favor both extremes over the intermediate types. This is called disruptive selection. A final theoretical possibility is for there to be no relation between fitness and the character in question: then natural selection is not acting on it. The biologist **Richard Lewontin** reminds us that not all aspects of an organism can be explained by natural selection.

An example of disruptive selection: bristles on fruit flies

In nature, sexual dimorphism is probably a common example of disruptive selection; but here we shall use an experiment by Thoday and Gibson on the *Drosophila melangaster* fruit fly as an example.

Thoday and Gibson bred from fruitflies with high, or low, numbers of bristles on a certain region of the body; individuals with intermediate numbers of bristles were prevented from breeding. As the graph shows, after 12 generations of this disruptive selection, the population had noticeably diverged. Disruptive selection is of particular theoretical interest, both because it can increase the genetic diversity of a population and promote speciation.

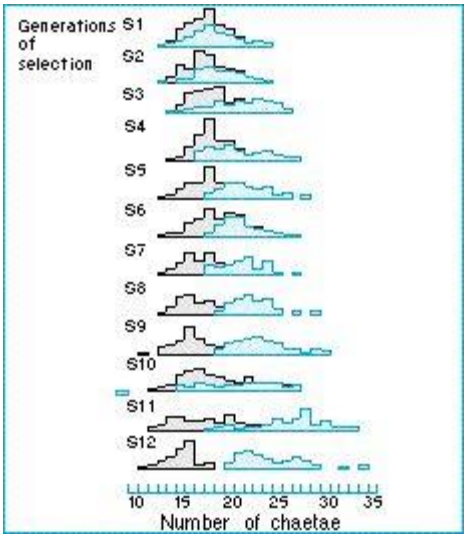

Figure: experimental disruptive selection on sternopleural bristle number in fruitflies. Individuals with many or few bristles were allowed to breed, those with intermediate numbers were not; and the population rapidly diverged. After Thoday & Gibson (1962).

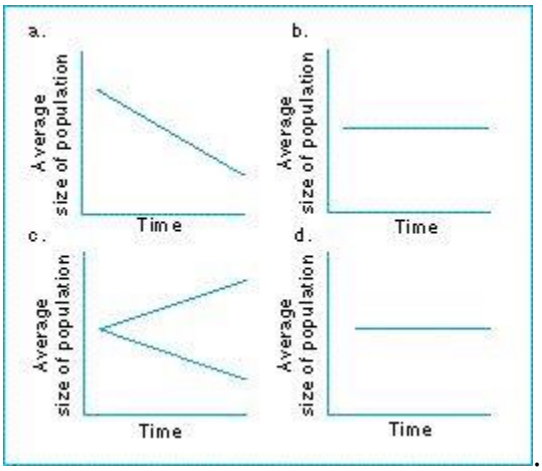

Figure: different kinds of selection result in different effects upon characters such as body size. (a) is directional selection (b) is stabilizing selection (c) is disruptive selection and (d) is no selection at all on the character's size.

"One has to distinguish natural selection for something and natural selection of something.

Natural selection did not select our blood to be red. It selected it for haemoglobin perhaps which happens to be red, but the redness itself was not selected. One of the problems of understanding evolution is deciding what characters are epiphenomenal accidental consequences of things, and which are the direct objects of natural selection. All we can do there is tell stories." Richard Lewontin.

How do populations show variation?

Organisms show variety at a number of different levels:

1. The morphologic level

At this level, the individuals of a natural population will be found to vary for almost any character we may measure. Pictured opposite: a much-studied instance of variation is shell color in the common snail *Cepaea nemoralis*.

• **Continuous variation**

In some characters, like body size, every individual differs from every other individual.

• **Discrete variation**

Other characters fall into a limited number of categories. Within the peppered moth population, for example, there are two main wing color forms (the dark, melanic form and the light, peppered form). A population that contains more than one recognizable form is polymorphic. As the number of forms in the population increases, the polymorphic, categoric kind of variation blurs into the continuous kind of variation.

2. The cellular level

At this level, such as the number and structure of chromosomes, we again find variation. Chromosomes can vary in their banding patterns (the order of genes) and individuals can vary in their number of chromosomes. At the DNA level the greatest amount of variation is found: DNA sequencing has shown that two individuals with indistinguishable phenotypes can have different genetic make-ups.

In natural populations the requirement of variation, as well as of reproduction and heredity, is met at all levels. However, if natural selection is to take place there must not only be variation: the variation must be for fitness.

Variation in biology can take two meanings:

• Firstly, it can refer to the characters of an organism which can vary among individuals at both the phenotypic and the genetic levels.

• Secondly, biologists talk about the variation in the fitness of individuals. For natural selection to take place, there must not only be variation in characteristics: the variation must be for fitness.

It is another condition of natural selection that the characteristics and hence the fitness of organisms is heritable. Not all characteristics of organisms are inherited and natural selection will not adjust the frequency of non-inherited characters. But many are inherited, on this natural selection can potentially work. Since inheritance is produced through genes via the Mendelian process, there must be sufficient genetic variation for natural selection to operate.

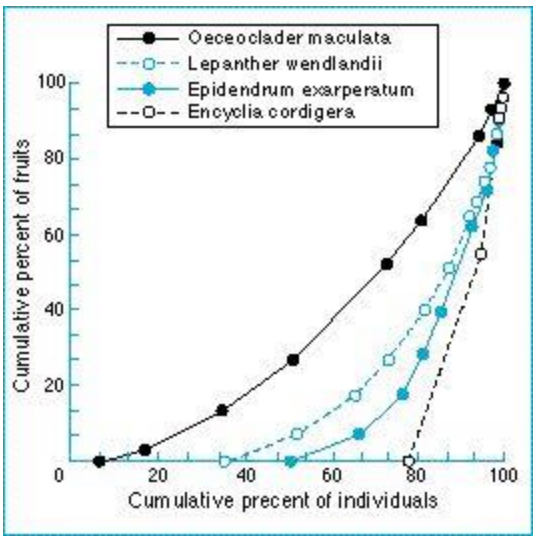

Figure: Variation in reproductive success within populations, illustrated by four species of orchid. The graphs plot the cumulative percentage of offspring produced, with the individual plants ranked from the least to the most successful. For example, in *Epdendrum exasperatum*, the least successful 50% of individuals produce none of the offspring, the next 17% of individuals produce 5% of the offspring, and so on. If every individual produced the same number of offspring the cumulative percentage graph would be the 45-degree line. From Calvo (1990).

What is the source of new variation?

Where does variation come from?

The extent of variation in natural populations is such that every individual must be genetically unique. Evolution from the origin, to the modern diversity, of life must have required more variation than existed in the original population. Where did the extra variation come from?

Several processes can generate new variation in a population.

• **Recombination** between chromosomes produces new chromosomes with their own unique sequences and many new genetic variants of a character like body size were probably generated by recombination.

• **Migration** is another important source of new genetic variation: when individuals arrive from distant parts, they will often have different genotypes from the local population; they thus provide new genetic variation.

Both recombination and migration work with existing allelic variation; they put existing variation into new genetic, or geographic, combinations. Important though this is, if there were no pre-existing allelic variation, recombination and migration would not generate new genetic variants. Recombination between identical chromosomes produces the same identical chromosomes over again.

• Mutation is the original source of genetic variation. Even in a population in which all copies of a chromosome were identical, new genetic variants would arise by mutation.

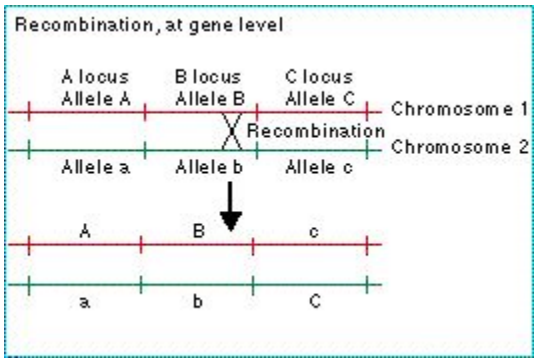

Figure: recombination at the gene level: the gene sequence in chromosome 1 changes from ABC to ABc: a new variant has been produced.

Mutation

A mutation is any change occurring in the message that a gene carry. Mutations mainly arise as copy errors when DNA is replicated at mitosis and meiosis. The fruitfly pictured here has suffered a dramatic mutation, called a macro mutation, and has an extra pair of wings. The first theoretician of mutation was H.J. Muller, who recognised that the rate of mutation in nature is extremely low, and that they are almost always deleterious to the fitness of the organism. The accumulation of deleterious mutations places a mutational load on the population.

However, Darwinian evolution requires a constant supply of variation: much of it is supplied by mutation. Mutation may occur at either chromosomal or base level, and the latter is illustrated in the following animation.

Mutations at the **base level** occur when there is a mistake in copying the genetic information. There are different types of mutation. **Synonymous mutations** - the base changes but the amino acid encoded does not. **In amino acid changing mutations**, a change in a base result in a different amino acid being encoded. In a **frame-shift mutation** a base is inserted with the result that the following bases are all a base further than their original position on the chromosome. In **a stop mutation** an amino acid encoding triplet mutates to a stop codon.

Are mutations adaptively directed?

The theory of directed variation

It is a deep property of Darwinism that the direction of evolution, particularly of adaptive evolution, is uncoupled from the direction of variation. When a new recombinant or mutant genotype arises, there is no tendency for it to arise in the direction of improved adaptation. Natural selection imposes direction on evolution, using undirected variation. An alternative viewpoint is the theory of directed variation.

What's wrong with the theory of directed variation?

If we reflect on the kind of mechanism that would be needed, it becomes clear that an adaptively directed mutation would be practically impossible. The organism would have to recognize that the environment had changed, work out what change was needed to adapt to the new conditions, and then cause the correct base changes in the relevant parts of its DNA. It would have to do so for an environment the species had never previously experienced.

It would be like humans describing subject-matter they had never encountered before in a language they did not understand: like a 17th century American using Egyptian hieroglyphics to describe how to change a computer program. (Hieroglyphics were not deciphered until the discovery of the Rosetta Stone in 1799.)

Even if it is just possible to imagine, as an extreme theoretical possibility, directed mutations in the case of moth coloration, the changes in the evolution of a more complex organ (like the brain, or circulatory system, or eye) would require a near miracle. It is for this reason that mutation is thought not to be directed toward adaptation.

Summary

• Organisms produce many more offspring than can survive, which results in a 'struggle for existence', or competition to survive.

• Natural selection will operate among any entities that reproduce, show inheritance of their characteristics from one generation to the next, and vary in 'fitness' (i.e., the relative number of offspring they produce) according to the characteristics they possess.

• The increase in frequency of the melanic, relative to the light colored, form of the peppered moth *Biston betularia* clearly illustrates how natural selection causes both evolutionary change and the evolution of adaptation.

• Selection may be directional, stabilizing, or disruptive.

• The members of natural populations vary with respect to characteristics at all levels. They differ in their morphology, their microscopic structure, their chromosomes, the amino acid sequences of their proteins, and in the DNA sequences.

• The members of natural populations vary in their reproductive success: some individuals leave no offspring; others leave many more than average.

• In Darwin's theory, the direction of evolution, particularly of adaptive evolution, is uncoupled from the direction of variation. The new variation that is created by recombination and mutation is accidental, and adaptively random in direction.

• Two reasons suggest that neither recombination nor mutation can alone change a population in the direction of improved adaptation: there is no evidence that mutations occur particularly in the direction of novel adaptive requirements, and it is theoretically difficult to see how any genetic mechanism could have the foresight to direct mutations in this way.

Muhammad Irfan

M.Sc. Zoology (2018-2020)

Govt. College Of Science Wahdat Road, Lahore.